ARCTIC
VOL. 65, NO. 1 (MARCH 2012) P. 13–34

Winter Movements of Bowhead Whales (*Balaena mysticetus*) in the Bering Sea

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(*Received 7 April 2011; accepted in revised form 23 June 2011*)

ABSTRACT. Working with subsistence whale hunters, we tagged bowhead whales (*Balaena mysticetus*) with satellite-linked transmitters and documented their movements in the Bering Sea during two winters. We followed 11 whales through the winter of 2008–09 and 10 whales in 2009–10. The average date that bowhead whales entered the Bering Sea was 14 December in 2008 and 26 November in 2009. All but one tagged whale entered the Bering Sea west of Big Diomede Island. In the winter of 2008–09, whales were distributed in a line extending from the Bering Strait to Cape Navarin, whereas in 2009–10, the distribution shifted south of St. Lawrence Island, extending from Cape Navarin to St. Matthew Island. Bowhead whales were most likely to be found in areas with 90%–100% sea-ice concentration and were generally located far from the ice edge and polynyas. The average date whales left the Bering Sea was 12 April in 2009 and 22 April in 2010. During the spring migration, all whales but one traveled north along the Alaska coast to summering grounds in the Canadian Beaufort. The remaining whale migrated a month later and traveled up the northern coast of Chukotka, where it was located when the tag stopped transmitting in August. It is unlikely that this whale migrated to the Beaufort Sea before returning south to winter within the Bering Sea, indicating the movements of bowhead whales are more complex than generally believed. Declining sea ice in the Bering Sea may result in the expansion of commercial fisheriesand shipping; areas where such activities may overlap the winter range of bowhead whales include the Bering and Anadyr straits, the eastern edge of Anadyr Bay, and St. Matthew Island.

Key words: bowhead whale, *Balaena mysticetus*, satellite telemetry, Bering Sea, shipping lanes, kernel density

RÉSUMÉ. Avec l'aide de pêcheurs de baleine de subsistance, nous avons marqué des baleines boréales (*Balaena mysticetus*) au moyen de transmetteurs en liaison avec un satellite et répertorié leurs mouvements au cours de deux hivers dans la mer de Béring. Nous avons suivi 11 baleines pendant l'hiver 2008-2009 et dix baleines en 2009-2010. En 2008, les baleines boréales sont entrées dans la mer de Béring le 14 décembre en moyenne, tandis qu'en 2009, elles sont arrivées le 26 novembre. À l'exception d'une baleine, toutes les baleines marquées ayant pénétré dans la mer de Béring sont passées par l'ouest de la grande île Diomède. À l'hiver 2008-2009, le parcours des baleines s'étendait en ligne depuis le détroit de Béring jusqu'au cap Navarin, tandis qu'en 2009-2010, le parcours s'est déplacé vers le sud de l'île Saint-Laurent, s'étendant ainsi du cap Navarin jusqu'à l'île Saint-Mathieu. Les baleines boréales étaient plus susceptibles de se retrouver dans les endroits dont la glace de mer a une concentration allant de 90 à 100 %. Généralement, elles se tiennent loin des lisières de glace et des polynies. En 2009, la date moyenne à laquelle les baleines ont quitté la mer de Beaufort était le 12 avril, tandis qu'en 2010, cette date était le 22 avril. Pendant la migration printanière, toutes les baleines, sauf une, se sont déplacées vers le nord le long de la côte de l'Alaska pour se rendre à leur aire d'estivage dans la partie canadienne de Beaufort. L'autre baleine a fait sa migration un mois plus tard et s'est déplacée le long de la côte nord de Tchoukotka, là où elle avait été repérée lorsque son marqueur a cessé ses transmissions en août. Il est improbable que cette baleine ait migré dans la mer de Beaufort avant de revenir vers le sud pour passer l'hiver dans la mer de Béring, ce qui indique que les mouvements des baleines boréales sont plus complexes qu'on ne le croyait antérieurement. La perte de glace de mer dans la mer de Béring pourrait se traduire par l'intensification des activités de pêche commerciale et d'expédition de marchandises. Les endroits où ces activités pourraient chevaucher le parcours d'hiver des baleines boréales comprennent les détroits de Béring et d'Anadyr, le côté est de la baie d'Anadyr et l'île Saint-Mathieu.

Mots clés : baleine boréale, *Balaena mysticetus*, télémétrie satellitaire, mer de Béring, routes maritimes, densité des noyaux

Traduit pour la revue *Arctic* par Nicole Giguère.

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INTRODUCTION

The annual range of the Western Arctic stock of bowhead whales (*Balaena mysticetus*), also known as the Bering-Chukchi-Beaufort (BCB) stock, within the Bering Sea is poorly understood. According to commercial whaling records, bowhead whales once summered throughout the northern Bering Sea, mostly west of St. Lawrence Island, Alaska (171˚W longitude) (Bockstoce and Botkin, 1980; Bockstoce et al., 2005). Commercial whaling began in 1849, and within 40 years, bowhead whales that summered in the Bering Sea were either extirpated or displaced to summering grounds in the Chukchi or Beaufort seas (Bockstoce et al., 2005). Although a few bowhead whales are observed along the southern Chukotka Peninsula in summer (Zelensky et al., 1997), the modern distribution of bowhead whales in the Bering Sea is largely limited to winter.

Today, most of the Western Arctic stock is thought to leave the Bering Sea each spring, migrating north along the coast of Alaska, past Point Barrow, and east into the Beaufort Sea (Moore and Reeves, 1993: Fig. 9.7). Native whalers observe bowhead whales passing by St. Lawrence Island between late March and April, with a few observations in May (Noongwook et al., 2007; Fig. 1). Most whales are believed to pass west of the Diomede Islands as they head north through the Bering Strait (Braham et al., 1979, 1980a). By early June, most whales have passed by Point Barrow (George et al., 2004) on their way to the Canadian Beaufort.

Rather than migrate east to the Beaufort Sea in spring, some whales may migrate to the Chukchi Sea or remain in the northern Bering Sea. Braham et al. (1980a:39) reported that "some Eskimo whalers suggest that a segment of the bowhead population moves northwestward from the Bering Strait into the western Chukchi Sea in spring," but they thought this unlikely because the ice north of the Chukotka Peninsula is heavy in spring. More recently, several studies have reported bowhead whales migrating up the western side of the Bering Strait in late May and June (e.g., Melnikov and Bobkov, 1993; Melnikov et al., 2004; Melnikov and Zeh, 2007). The timing of these movements makes it unlikely that these whales migrate past Point Barrow (Melnikov and Zeh, 2007).

After summering in the Beaufort or the Chukchi Sea, bowhead whales are believed to migrate south along the Chukotka Peninsula between August and November (Bogoslovskaya et al., 1982; Bessonov et al., 1990; Moore and Reeves, 1993: Fig. 9.7; Quakenbush et al., 2010). Bessonov et al. (1990) reported that bowhead whales pass through the Bering Strait, returning to the Bering Sea, in late October and early November, arriving at Sireniki in mid-November. Whales are again observed by Alaska Natives near St. Lawrence Island between December and February (Noongwook et al., 2007).

Factors that determine the winter distribution of bowhead whales within the Bering Sea are largely unknown. Sea ice is generally assumed to affect the movements of bowhead whales; advancing sea ice in the fall may force bowhead whales out of the Chukchi Sea and into the Bering Sea (e.g., Bogoslovskaya et al., 1982), and retreating sea ice in spring may initiate the spring migration (e.g., Braham et al., 1980a). During heavy-ice years, whales may be pushed as far south as the Pribilof Islands (Braham et al., 1980b). Polynyas, areas of open water usually formed downwind from land masses (Niebauer and Schell, 1993; Fig. 1), are generally believed to be important for bowhead whales because they provide open water for surfacing (e.g., Brueggeman et al., 1987). Whales have been observed within the Sirenikovskaya polynya from October to April (Bogoslovskaya et al., 1982; Zelensky et al., 1997; Fig. 1). They have also been seen in winter adjacent to the St. Lawrence Island and St. Matthew Island polynyas (Brueggeman, 1982; Brueggeman et al., 1984), within the fractured ice of the Anadyr Strait, and along the southern edge of the sea ice (Braham et al., 1980a; Brueggeman, 1982). In general, bowhead whales are not observed south of the marginal ice front (Ljungblad, 1986).

Although the winter distribution of bowhead whales appears to be associated with sea ice, attempts to model whale locations in the Bering Sea as a function of ice coverage have been largely unsuccessful (see Brueggeman et al., 1987), and it is likely that other factors, such as age, reproductive status, or prey availability, also influence whale movements. During both spring and fall, whales apparently migrate in distinct "waves" or "pulses" segregated by size (i.e., age). In spring, Noongwook et al. (2007) noted that smaller whales, likely yearlings, migrate past St. Lawrence Island first, then mid-sized whales, and finally the largest whales, including cows with calves. Similar segregation is observed during population counts at Point Barrow in spring (e.g., Braham et al., 1980b; Nerini et al., 1987). The fall migration, like the spring migration, appears to be segregated by size. In general, the largest whales arrive at St. Lawrence Island first, and the smallest whales, likely yearlings, arrive last (Noongwook et al., 2007), although such patterns are not observed near Sireniki, Russia (Bogoslovskaya et al., 1982).

Movements may also be dependent upon reproductive status. Although mating behavior has been observed almost year-round, data on fetus size indicate that conception probably occurs in late winter or spring (Koski et al., 1993; Reese et al., 2001), while bowhead whales are in the Bering Sea. Observations of mating behavior in winter are scant, but mating behavior has been observed near Southwest Cape on St. Lawrence Island (Braham et al., 1980b; Noongwook et al., 2007) and near St. Matthew Island (Braham et al., 1980b; Ljungblad, 1986). Calves are probably born between April and early June (Koski et al., 1993), during the spring migration, when whales are between the northern Bering Sea and Barrow (North Slope Borough, unpubl. notes, G. Noongwook, pers. obs.). Bogoslovskaya et al. (1982) report observations of calving within the Sirenikovskaya polynya. Subsistence whalers on St. Lawrence Island observe mothers with calves traveling as part of a "large-whale group," and calves are observed between April and June, most commonly in May (Noongwook et al., 2007).

FIG. 1. Study area of satellite-tracked bowhead whales in the northern Bering Sea. Blue dotted lines denote approximate boundaries of recurring polynyas, and the red solid line is the 200 m isobath.

The Bering Sea was generally not believed to be important for winter feeding (Lowry and Frost, 1984; Lowry, 1993), but this view was based on little evidence. Ljungblad (1986) observed whales resting, swimming, or possibly mating near St. Matthew Island in 1986, but observed no feeding behavior. Lowry and Frost (1984) and Lowry (1993) speculated that winter feeding in the Bering Sea was likely not significantin the annual nutrition cycle of bowhead whales. However, stable isotope ratios from the muscle and baleen of harvested whales suggest that significant feeding occurs within the Bering and Chukchi seas (Lee et al., 2005), and Noongwook et al. (2007) report feeding behavior along the southwest coast of St. Lawrence Island. Hazard and Lowry (1984) report on the stomach contents of a single whale harvested on St. Lawrence Island in May 1984; this whale's stomach contained evidence of feeding (mostly gammarid amphipods). Sheffield and George (2009) used stomach samples to classify the feeding status of 25 bowhead whales harvested between 1972 and 2009 at St. Lawrence Island (including data from Hazard and Lowry, 1984). Three of three (100%) whales harvested in fall had been feeding (mostly on euphausiids), and eight of 22 (36%) whales harvested in spring had been feeding (mostly on copepods). Hence, feeding in the Bering Sea is likely significant, at least in the vicinity of St. Lawrence Island.

In short, although bowhead whales spend up to six months per year (~November to April) in the Bering Sea, relatively little is known about their movements and distribution there. Knowledge of winter movements is based largely on observations from shore at a few locations (e.g., St. Lawerence Island, Sireniki, Cape Pe'ek) and on limited aerial and ship-based surveys. Movements of bowhead whales may be affected by sea ice, but also may be related to age, breeding status, or the distribution of prey in the Bering Sea.

Describing the winter distribution and movements of bowhead whales is important because commercial and industrial activities are increasing in the Bering Sea and will likely continue to increase as sea ice decreases in extent and thickness throughout the Arctic. Ships that use the Northern Sea Route (along the northern Russian coast) and the Northwest Passage (along the northern Alaska coast and through the Canadian Archipelago) must pass through the Bering Sea and Bering Strait. Shipping related to petroleum exploration and tourism are also expected to increase (ACIA, 2005; Treadwell, 2008). The Bering Sea crab fishery may expand northward as ice forms later and retreats earlier in the season, increasing its overlap with the bowhead winter range. Ship strikes and entanglement in fishing gear are major sources of mortality for North Atlantic right whales (*Eubalaena glacialis*) (Knowlton and Kraus, 2001) and could cause mortality of bowhead whales in the Bering Sea. Hence, collecting information on the distribution and movements of bowhead whales is important for the conservation of this species.

In this study, we describe the distribution and movements of 21 bowhead whales tagged with satellite-linked transmitters in the Bering Sea during the winters of 2008–09 and 2009–10. We present the timing and paths of the fall and spring migrations in relation to sea-ice concentration. Our primary goals are to document the winter distribution of bowhead whales in the Bering Sea and to provide information useful for charting shipping lanes and planning expansion of commercial fisheries. Thus, analyses of resource selection or dive behavior are outside the scope of this manuscript.

METHODS

Tagging

We used the satellite-linked transmitter attachment and deployment system developed by the Greenland Institute of Natural Resources (Heide-Jørgensen et al., 2001, 2003) to deploy tags on bowhead whales and the Argos system of satellites to obtain data from the tags. We used two types of tags: the SPOT tag, from which only estimated locations of whales are obtained, and the SPLASH tag, from which both estimated locations and dive behavior are obtained; both types of tags were manufactured by Wildlife Computers (Redmond, Washington, USA). The dimensions of both SPOT and SPLASH tags are described in Quakenbush et al. (2010). Tags were deployed using a 2 m or 4 m long fiberglass pole as a jab-stick (Heide-Jorgensen et al., 2003). The pole system included a biopsy tip designed to collect a skin biopsy during tag deployment; skin biopsies were used to determine the sex of whales, using PCR to amplify either zinc finger(ZFX and ZFY) genes (Morin et al., 2005) or USP9X and USP9Y genes (Bickham et al., 2011), both of which are sex-determining regions within bowhead whale DNA. Whale length was estimated visually by Native whalers at the time of tagging. Because of permit requirements, we avoided calves less than 1 year of age and cows with calves. All 21 tags used in this study were deployed in fall, three near Atkinson Point, Canada (69.94°N, 131.42°W), and 18 near Point Barrow, Alaska (71.29° N, 156.79° W).

Location Processing

Transmitter locations were estimated using signals received by Argos satellites while whales were at the surface. Location error is estimated by the Argos system and characterized by "location classes" (see the Argos User's Manual for a complete description; available from argos-system.org/manual/). Location classes are only an approximation of location accuracy (e.g., Vincent et al., 2002). Instead of using only the locations representing the highest accuracy (class 2 or 3), we chose to use all available location classes (B, A, 0, 1, 2, 3) and remove less accurate locations with a filterdeveloped by Freitas et al. (2008) in R version 2.5.1 (R Development Core Team, 2007).

Bowhead whale locations that resulted in swim velocities of over 1.94 m/s were removed unless they were within 5 km of the previous location. The threshold velocity of 1.94 m/s is the maximum observed migration speed of bowheads not fleeingvessels or assisted by currents (e.g., Zeh et al., 1993). The filteralso has an angular component to account for locations with a high degree of location error that often fall far from the line of travel, forming acute angles between adjacent locations (e.g., Freitas et al., 2008; Keating, 1994). We used default settings to definethe angular components of the Freitas et al. (2008) filter; within 2.5 km of the track line, locations resulting in angles less than 15° were removed and locations between 2.5 and 5 km of the track line were removed if they resulted in angles under 25°. We then removed locations that fell on land to establish the final set of locations used in our analyses.

Migration Paths

Whale locations were plotted in ArcMap 10 and we used the "points to line" tool to combine locations into tracks. We estimated the date on which whales entered the Bering Sea as the day when they passed south of the Diomede Islands (65.75°N; Fig. 1); this procedure was repeated for whales leaving the Bering Sea in spring.

Areas of Concentrated Use (Kernel Density Estimation)

We used kernel densities to identify geographic areas associated with a high probability of use by bowhead whales (e.g., Silverman, 1986; Worton, 1989; Wand and Jones, 1995). Kernel density estimation is a non-parametric method for calculating the probability that an animal occurs within each point in space. When calculating a kernel density, we overlay each location with a 2-dimensional probability density function (PDF), known as a kernel function. For example, a "normal" kernel is based on a normal probability density function, in which the shape of the kernel is described by a mean and a variance. For each dimension, the mean of the kernel is equal to the point location in that dimension (i.e., the latitude or longitude). However, because each kernel corresponds to a single location, the variance of the kernel, also known as the bandwidth, cannot be calculated using standard formulas for variance. Following Quakenbush et al. (2010), we selected a bandwidth matrix for each whale using Smoothed Cross-Validation (SCV; Duong and Hazelton, 2005) as calculated by package "ks" (Duong, 2007) in R version 2.11.1 (R Development Core Team, 2007). By fitting a full bandwidth matrix, we allowed the variance of the kernel to have different values in the x- and y-dimensions (i.e., longitude and latitude) and to covary. As recommended by Duong and Hazelton (2005), we pre-scaled our data before calculating bandwidth matrices.

Kernel densities are often described using percent probability contours, which are the contours that contain the desired percentage of total probability of use within the smallest area. For example, the 10% probability contour contains 10% of the probability of use within the smallest area on the surface of the kernel density. This definition results in an inverse relationship between the probability of finding a whale location and the value of the contour; i.e., a 10% probability contour contains only areas with a high probability of use, while a 90% probability contour contains areas with both high and low probabilities of use. If visualized in three dimensions, with the height of the kernel density surface representing probability of use, a 10% probability contour would surround the peak of the surface, whereas a 90% probability contour would be located lower on the surface and include the area within the contours above it.

When calculating kernel densities in practice, a study area is usually divided into grid cells within which individual kernels are summed. We overlaid the study area with a grid of 5 × 5 km cells that was large enough (321924 cells) to contain the complete kernel density for all whales. The grid had a modified Albers projection that was shifted west of the standard Alaska Albers projection; our projection had a central meridian of 170.0° W and standard parallels of 55° and 65° N latitude.

The number of locations per whale varied daily. To standardize the contributions of individual whales within a day, we split the day into four 6-hr periods and selected the location with the highest location class within each time period. When multiple locations within a time period had the same location class, we selected the location that was transmitted the earliest, thereby spacing the locations over time. We then generated a kernel density for each whale in each month of our analysis. To remove density that occurred on land, the kernel density was multiplied by a density that had cells coded 0 for land and 1 for water. We then rescaled the density for each whale so it integrated to 1.

Tags provided differing amounts of information regarding migration paths and areas of concentrated use because longevity and performance varied. We did not want tags that contributed little information to have equal weight in the kernel densities; therefore, we weighted the contribution of individual whales by the number of locations used to compute the kernel density for each whale within each month. Specifically, the kernel density within each grid cell was multiplied by the proportion of data contributed by each whale within each month. The cell densities for each whale were then summed to generate a single kernel density for all whales within each month during winter.

Monthly kernel densities were calculated for January, February, and March during the winter of 2008–09 and for November, December, January, February, and March during the winter of 2009–10. Kernel densities prior to January 2009 are presented in Quakenbush et al. (2010). These time periods correspond to the time when whales first entered the Bering Sea and extended to, but did not include, the month of April, when whales began to migrate, because migratory behavior is better described using track lines than kernel densities.

Sea Ice

Kernel densities were estimated on a monthly interval. To show how kernel density related to average sea-ice conditions, we overlaid kernel densities on maps of monthly average sea-ice concentration (%). To generate monthly average ice concentrations, we used data from the Advanced Microwave Scanning Radiometer (AMSR) instrument aboard NASA's Earth Observing System AQUA satellite (known as AMSR-EOS or, more commonly, AMSR-E). AMSR-E data are currently available through the National Snow and Ice Data Center at http://nsidc.org/data/amsre/. We calculated monthly average concentrations using a sample of daily ice concentrations and the "cell statistics" tool within ArcMap 10. Starting on the first day of each month, we sampled the ice concentrations every fourth day.

Sea-ice conditions are dynamic, and we do not expect average sea-ice concentration to illustrate sea-ice concentration on any specific day. Furthermore, while kernel densities illustrate areas associated with a high probability of use, they do not indicate sea-ice concentrations at the locations of individual whales. Therefore, we compared the concentration of sea ice where individual whales were located to that available within the winter range of bowhead whales. Using the same sample of days presented above (i.e., every fourth day, starting on the first day of each month), we extracted the percent sea-ice concentration at the highest quality location for each whale observed on that day. For the same sample of days, we also computed sea-ice concentration across an area that represents the general winter range of bowhead whales (Fig. 2). The winter range is approximate and serves to illustrate how sea-ice conditions within the Bering Sea change throughout the winter. We restricted the comparison to January, February, and March, as the Bering Sea is largely ice-free prior to January, and the spring migration begins in April. Our comparison of sea-ice concentration at whale locations versus an approximated winter range of the tagged whales is only descriptive, as a formal resource-selection analysis is beyond the scope of this paper. Sea-ice concentration alone probably cannot sufficiently explain where bowhead whale locations occur (Brueggeman et al., 1987), and few data exist for making more complex models of resource selection.

FIG. 2. Approximate winter range of tagged bowhead whales and the systematic random sample of whale locations for which ice statistics were summarized.

To describe bowhead locations relative to the marginal ice edge and polynyas, we used a smaller sample of AMSR-E ice concentrations. Starting with the first day of each month, we calculated the linear distance from each whale location to the marginal ice edge and nearest polynya every eighth day (i.e., four times each month for each whale). We defined the marginal ice edge as the southernmost limit of sea ice with greater than 90% sea-ice concentration. Polynyas were defined as areas with less than 90% sea-ice concentration that were north of the marginal ice edge.

RESULTS

Tagging

Fifteen tags were deployed in 2008, one in Canada and 14 in Alaska; of these tags, 11 transmitted long enough to enter the Bering Sea (Table 1). Fifteen tags were also deployed in 2009, four in Canada and 11 in Alaska; of these tags, 10 transmitted long enough to enter the Bering Sea (Table 2). Within the sample of 21 tagged whales, estimated lengths ranged from 8 to 15 m. Biopsies were collected for 14 whales, 9 males and 5 females (Tables 1 and 2).

Migratory Paths

During the winter of 2008–09, the 11 tagged whales entered the Bering Sea between 7 November and 11 January; the average entry date of these whales was 14 December (Table 1). All whales initially entered the Bering Sea between Cape Pe'ek and Big Diomede Island (Fig. 3). After passing south of Big Diomede, nine of the whales returned north of Big Diomede or Cape Pe'ek before resuming their southward movement. After passing south of Big Diomede for the last time, all 11 whales passed west of St. Lawrence Island through the Anadyr Strait (Fig. 4). One whale (B08-12) passed Sireniki (westbound) on 14 January and then returned (eastbound) on 16 January; however, whales generally did not enter the Gulf of Anadyr. All whales but two, B08-08 and B08-10, passed south of St. Lawrence Island by the end of January. B08-08 spent the entire winter north of

TABLE 1. Transmission statistics for 11 bowhead whales in the Bering Sea during the winter of 2008–09. The first and last dates of transmission south of the Diomede Islands in the Bering Strait (65.75˚ N) are termed 'Earliest' and 'Latest,' respectively. The average 'Latest' date was calculated only for the eight whales with transmitters that lasted until the spring migration. Dates are adjusted from GMT to Aleutian Standard Time, the local time zone.

Whale ID	PTT[1]	Type	Sex	Length (m)	Earliest	Latest	Days	# Locations	Lasted until spring migration?
B08-01	37233	SPLASH	F	11	27 December 08	13 April 09	107	114	Y
B08-03	37236	SPLASH	?	15	07 November 08	22 November 08	16	117	N
B08-06	37230	SPLASH	?	10	05 January 09	12 March 09	66	968	N
B08-07	37234	SPLASH	M	10	04 December 08	13 April 09	130	995	Y
B08-08	37277	SPLASH	?	10	27 December 08	31 March 09	94	661	Y
B08-09	37280	SPOT	M	9	06 December 08	15 April 09	130	543	Y
B08-10	50679	SPOT	F	10	11 January 09	09 April 09	88	1032	Y
B08-11	50685	SPOT	M	10	28 November 08	11 April 09	134	1221	Y
B08-12	60009	SPOT	M	> 9	06 January 09	27 April 09	111	780	Y
B08-13	60017	SPOT	?	10	05 December 08	12 March 09	97	427	N
B08-14	60018	SPLASH	M	> 14	28 November 08	11 April 09	134	684	Y
Average					μ = 14 December	μ = 12 April			
SD					σ = 21 d.	σ = 7 d.			

[1] PTT = Platform Transmitter Terminal.

TABLE 2. Transmission statistics for 10 bowhead whales in the Bering Sea during the winter of 2009–10. The first and last dates of transmission south of the Diomede Islands in the Bering Strait (65.75˚ N) are termed 'Earliest' and 'Latest,' respectively. The average 'Latest' date was calculated only for the eight whales with transmitters that lasted until the spring migration. Dates are adjusted from GMT to Aleutian Standard Time, the local time zone.

Whale ID	PTT[1]	Type	Sex	Length (m)	Earliest	Latest	Days	# Locations	Lasted until spring migration?
B09-01	37231	SPLASH	F	15	14 November 09	21 December 09	38	666	N
B09-02	37232	SPLASH	?	14	19 November 09	30 January 10	72	182	N
B09-03	93091	SPLASH	?	12	28 November 09	04 December 09	5	76	N
B09-04	93086	SPLASH	M	10	01 December 09	12 April 10	133	356	Y
B09-05	93078	SPLASH	M	10	25 November 09	10 April 10	135	501	Y
B09-08	42522	SPOT	M	14	29 November 09	21 January 10	53	18	N
B09-09	93089	SPLASH	?	14	25 November 09	26 May 10	181	871	Y
B09-13	93079	SPLASH	F	8	24 November 09	16 April 10	143	605	Y
B09-15	93085	SPLASH	F	11	27 November 09	16 April 10	140	301	Y
B09-16	33001	SPOT	M	13	04 December 09	22 April 10	139	342	Y
Average					μ = 26 November	μ = 22 April[1]			
SD					σ = 6 d.	σ = 17 d.[1]			
Average						μ = 15 April[2]			
SD						σ = 5 d.[2]			

[1] Average date and standard deviation include B09-09, the late migrating whale.
[2] Average date and standard deviation do not include B09-09, the late migrating whale.

St. Lawrence Island, moving within the Anadyr and Bering straits. After 25 February, B08-08 moved north to the Diomede Islands and remained near the Bering Strait until migrating north. B08-10 remained near the Anadyr Strait from 19 January until 17 March, when it passed south of St. Lawrence Island for the firsttime. This whale remained near Southwest Cape on St. Lawrence Island between 17 and 31 March, before migrating northward (Fig. 5). Northward migration began the firstweek in April. Again, all whales passed through the Anadyr Strait, west of St. Lawrence Island. Eight of 11 tagged whales that were tracked into the Bering Sea were monitored throughout the entire winter and passed north through the Bering Strait (defined as the day passing north of Little Diomede Island) over a four-week period from 31 March to 27 April (average = 12 April; Table 1). When leaving the Bering Sea, fivewhales passed east of Little Diomede and one passed west of Big Diomede (Fig. 5); no whales passed between Big and Little Diomede islands. Two whales did not transmit enough locations to indicate on which side of the Diomede Islands they migrated.

During the winter of 2009–10, the average date on which the 10 tagged whales initially entered the Bering Sea was 26 November, and the range of entry dates, from 14 November to 4 December, was smaller than in the previous year (Table 2). Nine whales initially entered the Bering Sea between Cape Pe'ek and the Diomede Islands, whereas one whale passed between Little Diomede and Wales (Fig. 3). After passing south of the Diomede Islands, four of 10 whales returned north of the Diomede Islands or Cape Pe'ek

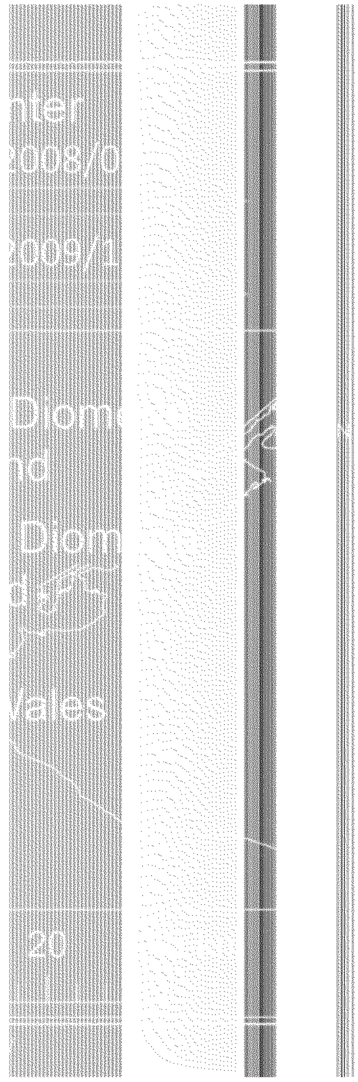

FIG. 3. Tracks of tagged bowhead whales moving south through the Bering Strait into the Bering Sea during the winters of 2008–09 (n = 11) and 2009–10 (n = 10). Dotted lines indicate connected locations that crossed landforms.

before resuming their southward movement. After passing south of the Diomede Islands the final time, eight whales passed west of St. Lawrence Island through the Anadyr Strait, whereas one whale passed east of St. Lawrence Island (Fig. 4); transmissions from one tagged whale ceased before it passed St. Lawrence Island. As in the winter of 2008–09, the majority of whales did not enter the Gulf of Anadyr. However, one whale (B09-01) passed Sireniki on 19 November and remained in the Gulf of Anadyr until approximately 30 November. In 2009–10, in contrast to the previous year, no whales wintered north of St. Lawrence Island. Seven of 10 whales spent time within 100 km of St. Matthew Island. Of the transmitters that lasted until the spring migration, five of six transmitted within 100 km of St. Matthew Island. As in spring 2009, northward migration in 2010 began during the first week of April. Six whales were monitored throughout the 2009–10 winter, and we determined that five passed north of the Diomede Islands between 10 and 22 April (average = 15 April), and one whale (B09-09) passed there much later, on 26 May (Table 2). Whereas the other five whales migrated towards Point Barrow, Alaska, this whale migrated northwestward, off the Chukotka coast, where it remained until the tag stopped transmitting in August (Fig. 6). B09-09 was also one of two whales in 2010 to migrate west of Big Diomede. In 2010, three whales migrated east of the Diomede Islands and one whale did not transmit enough locations to determine where it passed in relation to the Diomede Islands (Fig. 5).

Kernel Densities

Kernel densities for the winter of 2008–09 included locations from 10 whales in January, February, and March (Table 3). Kernel densities for the winter of 2009–10 included locations from 9 whales in November, 10 in December, 8 in January, and 6 in February and March (Table 3).

During the winter of 2008–09, whales were generally distributed along a line extending toward the southwest from the Bering Strait to an area east of Cape Navarin

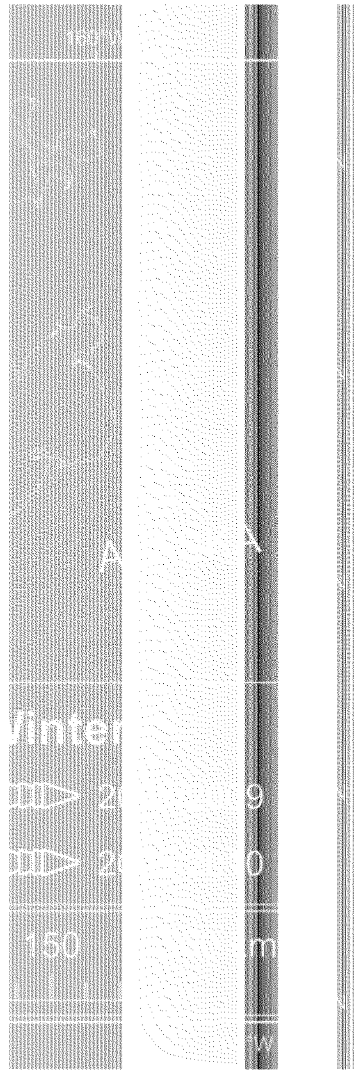

FIG. 4. Tracks of tagged bowhead whales within the Bering Sea during the winters of 2008–09 (n = 11) and 2009–10 (n = 10).

(Fig. 7). In January 2009, the kernel density of bowhead whale locations was distributed from the southern Chukchi Sea to approximately 100 km east of Cape Navarin (Fig. 7a), with the greatest use in areas of higher ice concentration (95–100%) and minimal use in areas of lower concentration (less than 90%) in the Gulf of Anadyr and south of St. Lawrence Island (Fig. 7b). In February 2009, the kernel density of whale locations extended ~100 km south of Cape Pe'ek to the 200 m bathymetric contour (Fig. 7c); again, areas with low average concentration (less than 90%) of sea ice were generally not used (Fig. 7d). The same general pattern relative to concentration of sea ice was observed in March 2009 as whales shifted to nearshore areas north and south of St. Lawrence Island and into the Bering Strait (Figs. 7e and 7f).

The density of whale locations differed markedly in the two winters studied. During November and December 2008, the whales remained largely in the Bering Strait, within 75 km of the Diomede Islands (Quakenbush et al., 2010); in those same months in 2009, they moved farther south into the Bering Sea. In November 2009, the density of whale locations was concentrated in the northern Bering Sea, north of St. Lawrence Island and in the northern Gulf of Anadyr (Fig. 8a) and largely corresponded with 20–60% average ice concentrations (Fig. 8b). In December 2009, the density of whale locations shifted southward (Fig. 8c) along with the southward advance of the sea ice (Fig. 8d). In January 2010, most whale locations were south of St. Lawrence Island and north of the 200 m isobath (Fig. 8e). In contrast with January 2009 (Fig. 7a), when whale locations extended from the Bering Strait south to Cape Navarin, whales in January 2010 were mostly south of St. Lawrence Island (Fig. 8e). Further, during January 2010, whales were located near areas of lighter ice concentration, such as the St. Lawrence and St. Matthew Island polynyas (Fig. 8e and 8f). In February 2010, however, the density of whale locations shifted south (Fig. 9a); some locations were even south of the 200 m isobath. The southward shift in whale locations was not due to the loss of two transmitters, B09-02 and B09-08, in February (Table 3), as both whales had traveled south to St. Matthew Island before contact was lost. No locations fell within the St. Lawrence Island or Sirenikovskaya polynyas; however, there were locations adjacent to

FIG. 5. Tracks of tagged bowhead whales moving north through the Bering Strait into the Chukchi Sea in April 2009 (n = 8) and 2010 (n = 6).

the St. Matthew Island polynya (Fig. 9b). In March 2010, the density of whale locations was concentrated to the north and west of St. Matthew Island and to the south and east of Cape Navarin (Fig. 9c). Although most locations were in regions with 95% to 100% ice concentration (Fig. 9d), some locations were in an area of low ice concentration beyond the 200 m isobath. In contrast to March 2009, there were no whale locations in the Anadyr Strait, near St. Lawrence Island, or within the Bering Strait (compare Figs. 7e and 9c). There was also more ice coverage in March 2010 (Fig. 9d) than in March 2009 (Fig. 7f). In March 2009, sea ice with over 95% concentration extended only as far south as St. Matthew Island (Fig. 9d), whereas in March 2010, sea-ice concentrations greater than 95% extended more than 150 km south of St. Matthew Island.

Summary of Ice Conditions

Percentages of ice concentration at bowhead locations were higher than average within the area where bowheads winter. During all months (January–March) of both winters, 69% to 100% of whale locations fell within the 90%–100% sea-ice concentration category (Fig. 10). Whale locations within the 0%–10% ice concentration category were found only in January and March 2010, even though 11%to 30% of the bowhead wintering area fell into that category. During the three winter months, ice concentration at bowhead locations averaged 98% (SD = 4.4) in 2009 and 94% (SD = 15.1)in 2010.

Distance to Marginal Ice Edge and Polynyas

Bowhead whale locations were generally north of the marginal ice edge, definedas the southernmost 90% sea-ice concentration contour. During the winter of 2008–09, bowhead whales were located an average of 334 km north of the marginal ice edge in January, 230 km north in February, and 226 km north in March. Only one location in the sample, from March 2009, was south (13 km) of the marginal ice edge. During the winter of 2009–10, bowhead whales were located an average of 94 km north of the marginal ice edge in January, 130 km in February, and 97 km

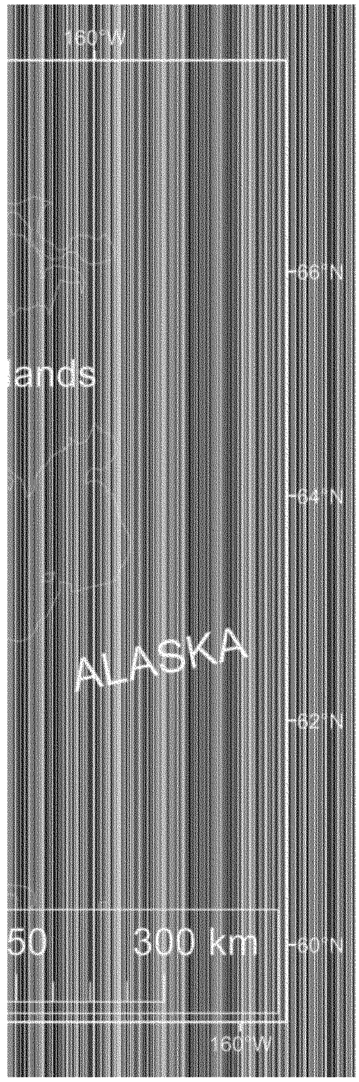

FIG. 6. Northern migration of tagged bowhead whale B09-09 during May and June 2010, from St. Matthew Island in the Bering Sea to the Chukchi Sea. This whale was tagged at Point Barrow, Alaska, on 29 August 2009.

in March. Five whale locations, representing four whales, were between 1 and 35 km south of the marginal ice edge in January 2010. One whale was located between 1 and 3 km south of the marginal ice edge twice in March 2010. The average distance of whales to the marginal ice edge was closer in the winter of 2009–10 than in 2008–09; the difference was 240 km in January, 100 km in February, and 129 km in March.

Bowhead whale locations were not typically found within polynyas, definedhere as areas north of the marginal ice edge with ice coverage of 90% or less. The average distance from whale locations to polynyas during the winter of 2008–09 was 104 km in January, 175 km in February, and 161 km in March (Table 4). Only 1 of 102 locations (i.e., ~1%) fell within a polynya during that winter: B08-10 was located 42 km within the St. Lawrence Island polynya in March 2009. The average distance from whale locations to polynyas during the winter of 2009–10 was 56 km in January, 150 km in February, and 174 km in March (Table 4). Only three of 53 sampled locations (~6%) fell within polynyas during the winter of 2009–10. Two whales, B09-13 and B09-16, were located 4 and 5 km within the St. Lawrence Island polynya, respectively, on 9 January 2010. One whale, B09-16, was located 3 km within the St. Lawrence Island polynya on 17 January 2010 (Table 4). The average distance of whales from polynyas was closer in two of three winter months in 2009–10 than in 2008–09. In January and February, whales were 48 km and 25 km closer to polynyas in 2010 than in 2009. In March, however, whales were 13 km farther from polynyas in 2010 than in 2009.

DISCUSSION

Our results provide the first description of bowhead whale distribution and movements in the Bering Sea based upon satellite tags. In general, our findings support those of prior studies (e.g., Bogoslovskaya et al., 1982; Brueggeman et al., 1984; Ljungblad, 1986) and traditional ecological

TABLE 3. The number of bowhead whale locations, for each whale, used to estimate monthly kernel densities for the winters of 2008 – 09 and 2009 – 10. Few whales entered the Bering Sea prior to January in the winter of 2008 – 09. November and December 2008 densities are provided in Quakenbush et al. (2010). One whale, B08-03, stopped transmitting in November 2008 and is not included in this table.

			Month				
Winter	Whale ID	PTT	November	December	January	February	March
2008 – 09	B08-01	37233			42	21	3
	B08-06	37230			105	100	47
	B08-07	37234			92	96	86
	B08-08	37277			81	90	77
	B08-09	37280			29	51	91
	B08-10	50679			88	84	106
	B08-11	50685			91	101	94
	B08-12	60009			71	67	62
	B08-13	60017			85	64	22
	B08-14	60018			90	73	60
2009 – 10	B09-01	37231	71	81			
	B09-02	37232	38	45	38		
	B09-03	93091	70	11			
	B09-04	93086	43	44	49	40	35
	B09-05	93078	55	60	61	42	38
	B09-08	42522		6	3		
	B09-09	93089	62	98	61	51	50
	B09-13	93079	42	88	67	35	53
	B09-15	93085	37	63	47	12	23
	B09-16	33001	33	34	34	46	14

knowledge (Braham et al., 1979; Noongwook et al., 2007). Tagged whales in our study occurred in the same general areas where bowheads have been observed during aerial and ship-board surveys, such as along the southern ice edge, in the Anadyr Strait, near St. Matthew and St. Lawrence islands (e.g., Brueggeman et al., 1984; Ljungblad, 1986), and near Sireniki (e.g., Bogoslovskaya et al., 1982). Tagged whales spent virtually no time east of St. Lawrence Island and most migrated through the Anadyr Strait, as has been reported for bowheads by Native subsistence whalers (Braham et al., 1979; Noongwook et al., 2007).

In contrast to the observations of subsistence whalers, however, we did not identify separate spring migratory paths near St. Lawrence Island from our tagged whale locations. Subsistence whalers on St. Lawrence Island have observed two migratory paths (Braham et al., 1980a, b, 1984; Noongwook et al., 2007). Whales hunted at Southwest Cape by hunters from Savoonga approach the cape from the east and then move offshore, towards Chukotka (Fig. 5). These whales are not believed to pass close by (within hunting range) of the village of Gambell. Whales hunted by whalers from Gambell pass Southwest Cape offshore and then approach shore, passing close to the village. Of our tagged whales, three passed southwest Cape during the spring migration, one in 2009 and two in 2010. Although one of these whales (B09-09) crossed the Anadyr Strait and migrated up the Russian coast, the other two did not (Figs. 5 and 6). In general, whales passing Southwest Cape were no farther offshore from Gambell than other whales, and separate migratory paths past Gambell were not apparent (Fig. 5).

One tagged whale (B09-09) migrated a month later than other tagged whales, passing Cape Pe'ek on 26 May (Fig. 6). This whale did not migrate to the Beaufort Sea, but remained along the Russian coast within the Chukchi Sea at least until its tag failed in August. In 2001, Melnikov and Zeh (2007) counted 470 (95% CL 332 to 665) bowhead whales passing Cape Pe'ek (Fig. 1) between 23 May and 14 June. That same year, the spring migration count at Barrow ended on 7 June, when the migration was believed to be over (George et al., 2004). Judging by travel velocities observed by Melnikov and Zeh (2007), few of the whales observed at Pe'ek in June could have migrated past Point Barrow during the survey. Melnikov and Zeh (2007) therefore suggested that the whales they observed were migrating to the Chukchi Sea, not the Canadian Beaufort. It is clear from the movements of B09-09 that some whales do not migrate past Barrow in spring and that spring migration counts at Barrow (e.g., Zeh et al., 1993; George et al., 2004) do not count the entire Western Arctic stock.

Interestingly, B09-09 was tagged near Point Barrow on 29 August 2009, yet nearly a year later this whale had not returned to Point Barrow. After summering along the northern coast of Chukotka, this whale was ~160 km northwest of the Diomede Islands on 21 August 2010 when its tag stopped transmitting. We do not know where B09-09 summered prior to being tagged near Point Barrow on 29 August 2009, but we believe that after spending the summer of 2010 in the Chukchi Sea, this whale likely did not return to Point Barrow before the fall migration in 2010. Thus, we suggest that some whales may not return to the same summering area each spring.

Movements Relative to Sea Ice

The distribution of tagged whales relative to ice conditions was not consistent with patterns found by previous studies in the Bering Sea. Surveys and shore-based

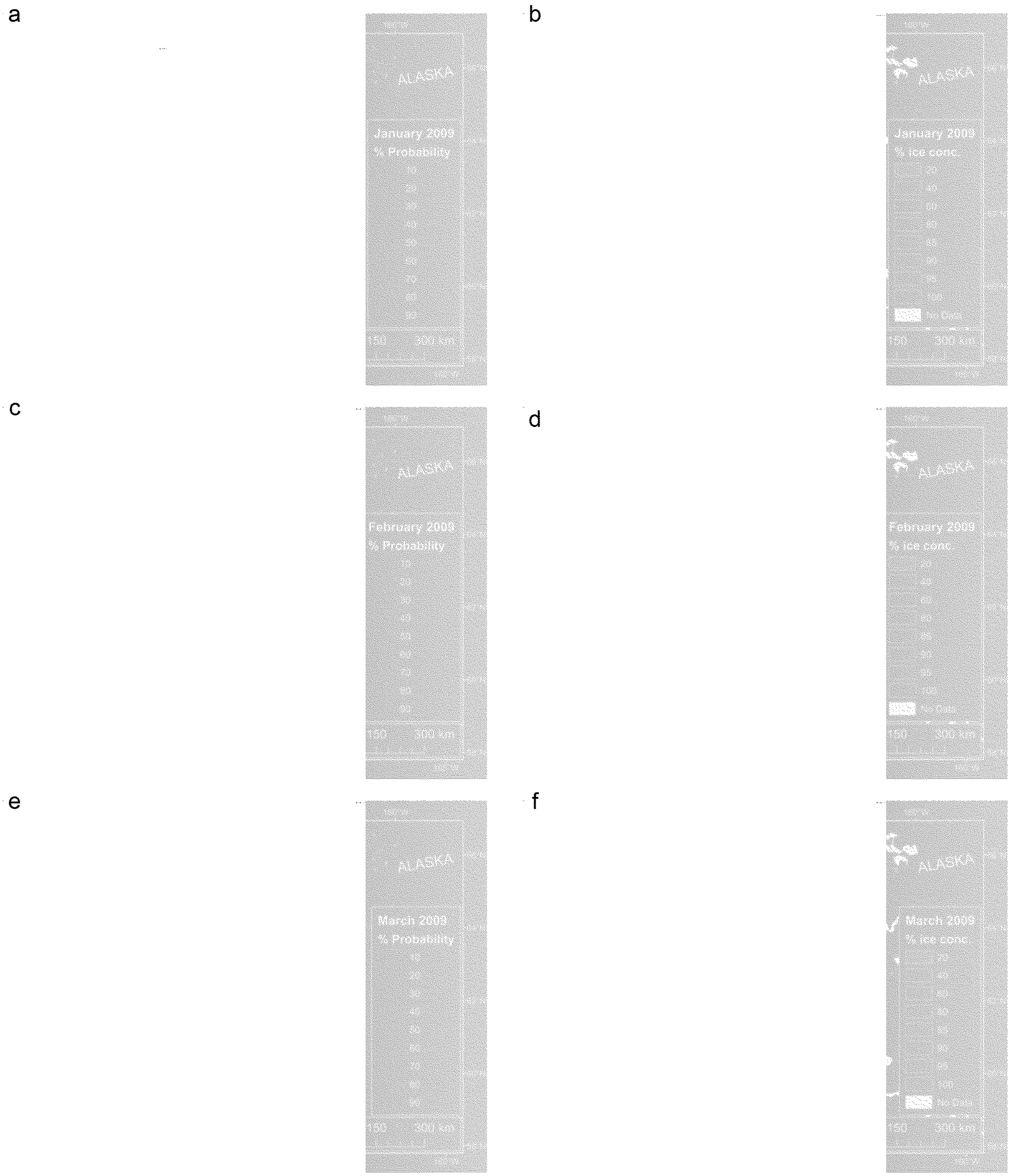

FIG. 7. Contours showing probability of use (%) by bowhead whales and average AMSR-E ice concentrations in January to March 2009. The ice concentration maps include non-shaded contours for probability of use, illustrating how probability of use overlaps ice concentration.

observations indicated that whales were associated with the marginal ice edge (Ljungblad, 1986) and with polynyas (Bogoslovskaya et al., 1982; Brueggeman et al., 1984). While tagged whales were sometimes found near the marginal ice edge and within polynyas, such locations were uncommon. Even though our sample sizes were limited, it is

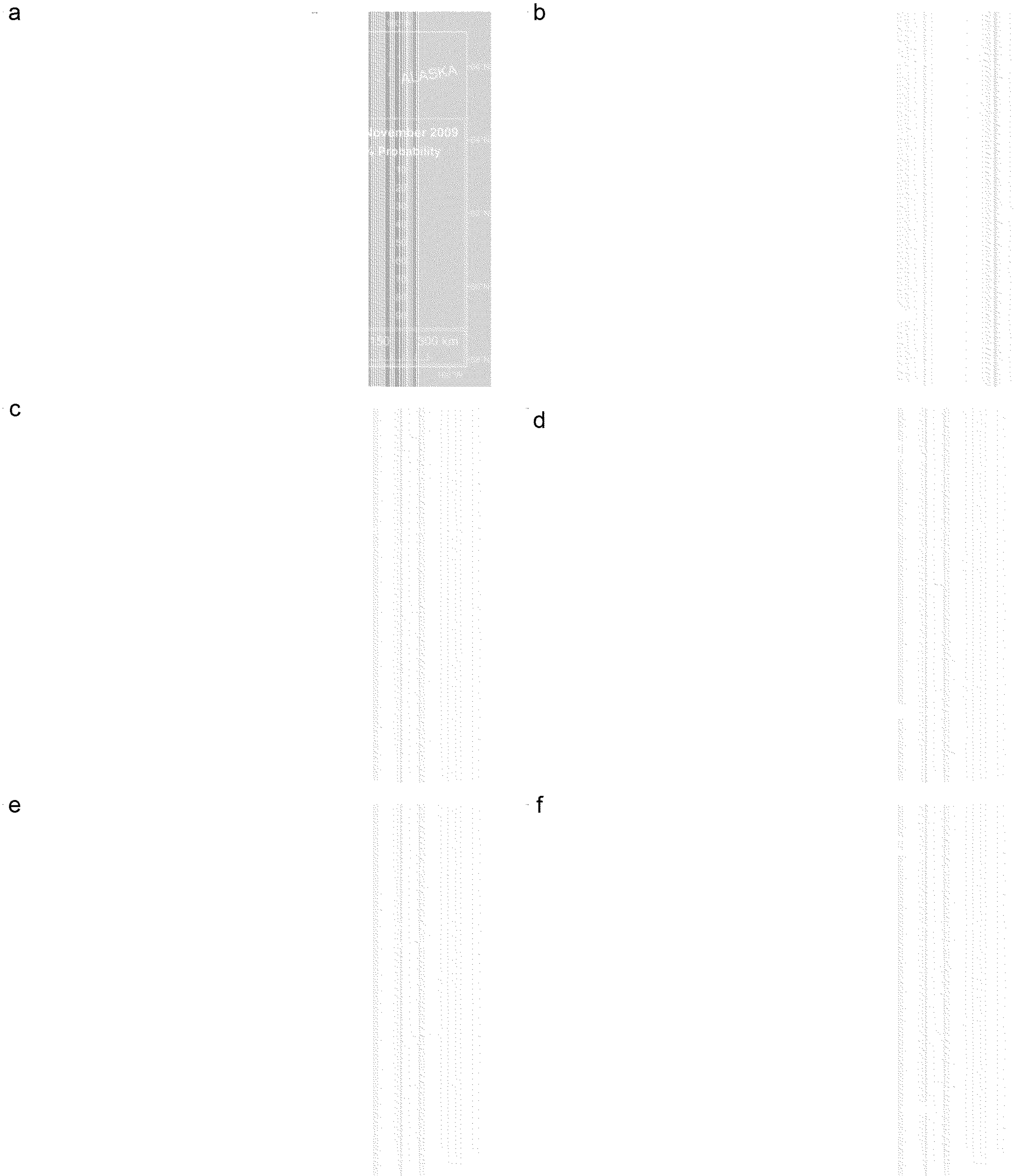

FIG. 8. Contours showing probability of use (%) by bowhead whales and average AMSR-E ice concentration from November 2009 to January 2010. The ice concentration maps include non-shaded contours for probability of use, illustrating how probability of use overlaps ice concentration.

unlikely that so few locations from tagged whales would be found near the marginal ice edge and polynyas if a substantial proportion of the population relied on those habitats.

Perhaps thicker sea ice once restricted bowhead whales to areas near open water. Although the extent of winter sea ice in the Bering Sea has not changed over time (Moore and a

b

c

d

FIG. 9. Contours showing probability of use (%) by bowhead whales and average AMSR-E ice concentration in February and March 2010. The ice concentration maps include non-shaded contours for probability of use, illustrating how probability of use overlaps ice concentration.

Laidre, 2006), the occurrence of multi-year ice is probably decreasing. Multi-year ice does not form in the Bering Sea, but drifts south through the Bering Strait. Multi-year ice is decreasing throughout the Arctic (ACIA, 2005; Nghiem et al., 2007; Perovich and Richter-Menge, 2009); therefore, less multi-year ice is expected to drift into the Bering Sea. Indeed, subsistence whalers at St. Lawrence Island have observed a decrease in multi-year ice and an increase in open water (Noongwook et al., 2007). Perhaps because of the changing ice conditions, whaling in late fall and winter has recently become common at St. Lawrence Island. Between 1974 and 1990, no whales were harvested in winter; however, between 1995 and 2005, roughly 40% of the whales harvested at St. Lawrence Island were taken in winter rather than in spring (Noongwook et al., 2007).

Fine-scale distribution of bowhead whales relative to sea-ice concentration in the Bering Sea was examined in two previous studies. Brueggeman (1982), using data from aerial surveys conducted in 1979, concluded that bowhead whales were most likely located in areas with ~38%–50% ice concentration. Brueggeman et al. (1987) used a larger data set, combining ship and aerial surveys conducted in 1979, 1983, and 1986. They observed bowhead whales in areas with 55%–95% ice concentration more frequently than expected given the ice concentrations were available along survey lines. In both studies, observers characterized the sea ice, which provided a better description of the sea-ice habitat than is possible from AMSR-E ice concentration. AMSR-E ice concentration data use a pixel size of 12.5 km, and the distribution of ice within a pixel is unknown. Also, thin ice, including grease ice (a thin, early stage of sea-ice development), is defined as ice cover within AMSR-E data, whereas Brueggeman et al. (1987) considered grease ice as open water. For these reasons, a direct comparison between ice coverage in our study and the small-scale visual observations of Brueggeman et al. (1987) is not possible.

The relationship between bowhead whale movements and sea ice was also studied for the Eastern Canada-West

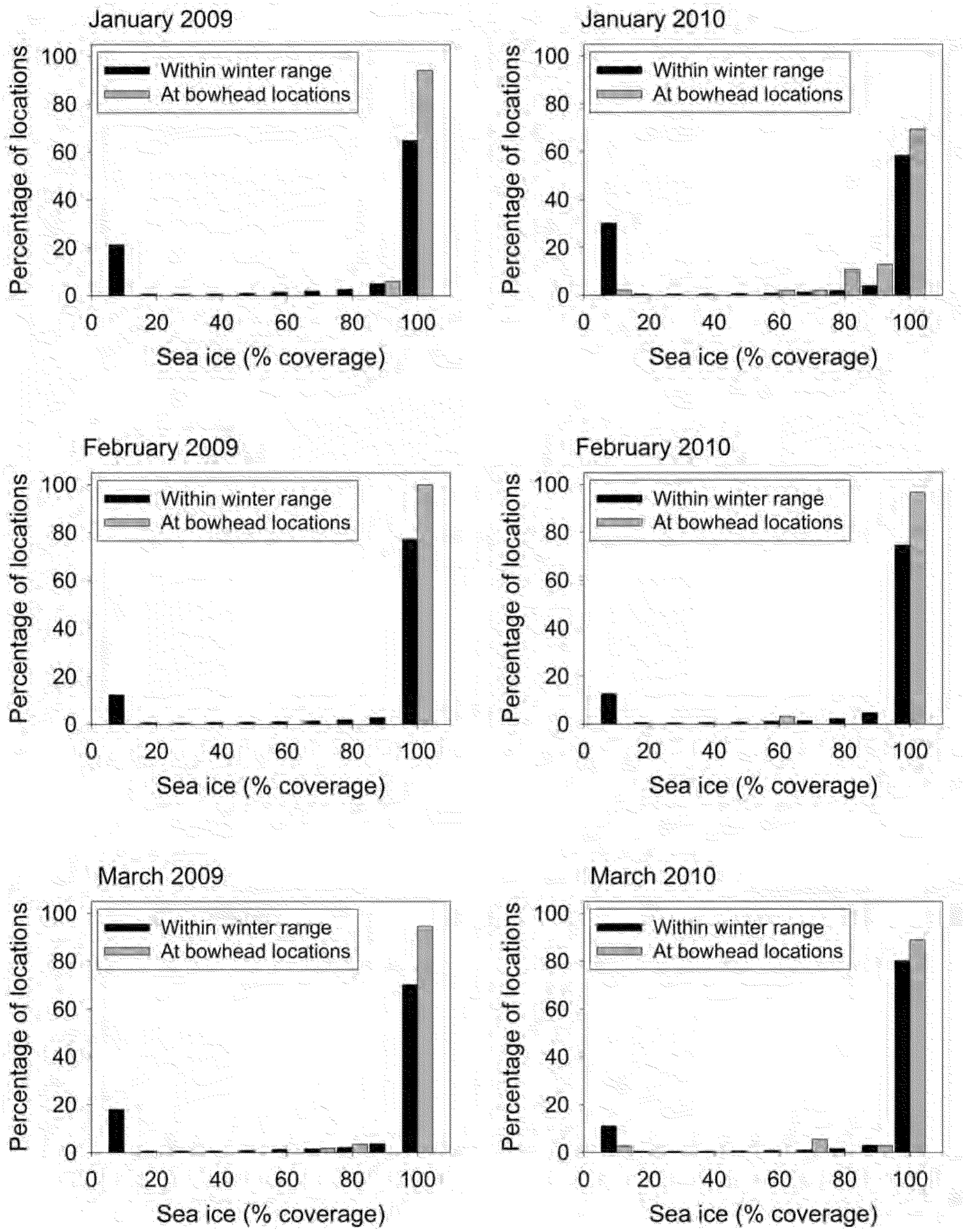

FIG. 10. Percent sea-ice concentration (12.5 km daily AMSR-E) at the random sample of bowhead whale locations presented in Figure 2 compared to all cells within winter range of bowhead whales in Bering Sea.

TABLE 4. Distances (km) of whale locations to the southern marginal ice edge and to polynyas within the Bering Sea during the winters of 2008–09 and 2009–10. Negative numbers (in parentheses) indicate a whale location south of the marginal ice edge or within a polynya.

		Distance to marginal ice edge (km)		Distance to nearest polynya (km)		Sample size (*n*)	
Winter	Month	Average	Range	Average	Range	Locations	Whales
2008–09	January	334	54–634	104	3–313	38	10
	February	230	14–554	175	12–399	34	10
	March	226	(-13)–635	161	(-42)–337	30	10
2009–10	January	94	(-35)–271	56	(-5)–149	22	8
	February	130	3–249	150	23–313	18	6
	March	97	(-3)–264	174	0–384	13	6

Greenland stock (Ferguson et al., 2010). During winter, bowhead whales coincided with pockets of low sea-ice concentration (35%–65%) and avoided areas with more than 65% ice concentration. In general, whales were within 300 km of the marginal ice edge. Ferguson et al. (2010) speculate that whales select lower ice concentrations near the marginal edge to reduce the risk of ice entrapment. We observed whales in areas of greater ice concentration (μ = 98% in 2009 and 94% in 2010) and farther from the marginal edge (Table 4) than those Ferguson et al. (2010) observed. We speculate that sea ice in the Bering Sea may be more dynamic and thinner than sea ice near the wintering grounds of the Eastern Canada-West Greenland stock. Polynyas in the Bering Sea are created largely by winds; although dominant north winds create polynyas on the southern sides of land forms, shifting winds can create open water almost anywhere within the Bering Sea. Furthermore, sea ice in the Bering Sea is predominantly first-year ice (Niebauer and Schell, 1993). Hence, we suspect that sea ice does not limit the distribution of whales within the Bering Sea as it may do in Eastern Canada.

The reason for between-year variability in the winter distribution of tagged whales is unclear. During the winter of 2008–09, whales were distributed roughly along a line extending from the Bering Strait down to an area east of Cape Navarin (Fig. 7). During the winter of 2009–10, the distribution of tagged whales was largely limited to the area south of St. Lawrence Island and extended from Cape Navarin to St. Matthew Island (Figs. 8 and 9). The difference in distribution between winters may be due to limited sample sizes, and we cannot rule out the possibility that whales were distributed throughout the Bering Sea in both winters. An alternative explanation is that the factors that influencebow-head distribution in winter, possibly the distribution of prey or ice thickness, differed between years. The distribution of whales was farther south in February and March of 2010 than in February and March of 2009, corresponding to a time when sea ice also extended farther south (compare Figs. 7 and 9). However, most whales were still far from the southern ice margin, and polynyas were still largely unused. Sea ice overlying the Anadyr Current is highly dynamic and fractured (e.g., Brueggeman et al., 1987). This current is believed to be consistently strong throughout the winter (Clement et al., 2005). In addition to providing bowhead whales with small leads for breathing, it may provide food by advecting zooplankton from the Bering Slope or Aleutian Basin (Berline et al., 2008). Bowhead whales were largely aligned with the Anadyr Current during the winter of 2008–09. While the bowhead distribution included the Anadyr Current in the winter of 2009–10, the whales also ranged farther east, towards St. Matthew Island. Although we would expect the Anadyr Current to provide similar resources in both winters, there is little information on the spatial or temporal variability in sea-ice thickness or zooplankton.

The different distributions in the two winters cannot be explained by whale age (length) or sex, either. Sample sizes are not large enough for statistical tests of how the distributions differed by sex or age; however, visual examination of the data revealed no patterns. For example, during the winter of 2008–09, no whales were observed closer than 100 km to St. Matthew Island. During the winter of 2009–10, the distribution of bowhead whales shifted east towards St. Matthew Island, and six whales were located within 100 km of that island. These whales ranged in length from 8 to 14 m; of those where sex was known, three were male and two were female. Hence, the whales that spent time near St. Matthew Island represented both sexes and virtually all sizes (Tables 1 and 2).

Limits of Inference

The distribution of whales with tags may be biased if tag transmission rates vary because of whale behavior or ice conditions. Tags must break the surface to transmit; because they are placed well behind the blowhole, we do not expect to receive transmissions when whales are in closed sea ice and push only their blowholes through the ice to breathe (e.g., George et al., 1989). While this behavior would bias our sample of locations away from areas with high ice coverage and towards areas with open water, we observed few locations in open water. It is also possible that pockets of open water in the sea ice may provide calm water and allow tags to surface more reliably than they might south of the marginal ice edge or within large polynyas. However, most whales were located far from polynyas and the marginal ice edge. There were also no obvious gaps in transmissions as whales approached ice margins, so there was no evidence to indicate that tags stopped transmitting as they approached open water. Hence, we suspect that location bias related to sea-ice conditions is minor.

While tags likely reflectthe movements of individual whales, we know that tagged whales do not represent the movements of the entire Western Arctic stock. In particular, we did not tag calves or whales with calves. If females with calves are spatially segregated within the winter range, our description of the winter range may be too small. Although our perception of the winter range of bowhead whales may expand if more bowhead whales are tagged in the future, we have probably described the most important wintering areas. Furthermore, identifying additional wintering areas will not decrease the importance of the areas we have described. The Bering and Anadyr straits, the area east of Cape Navarin, and St. Matthew Island are clearly important for the conservation of bowhead whales.

Crab Fishery

Approximately 10% of harvested whales have rope scars, indicating they survived a prior entanglement (North Slope Borough, unpubl. notes; J.C. George, pers. obs.), and stranding reports from the Alaska Region document three bowhead whale entanglements between 2003 and 2010 (NOAA Fisheries, 2011). Although the type of fishing gear is usually unknown, crab gear is most often identified (e.g., King, 1990; Philo et al., 1992; George, 2010). Two or three crab fisheriesmay overlap the distribution of bowhead whales in both time and space. The blue king crab (*Paralithodes platypus*) fishery is relatively small (total allowable catch ~ 726 thousand kg in 2010)and occurs approximately 80 km southwest of St. Matthew Island. In recent years, this fishery has opened on 15 October and closed on 1 February the following year; however, fishinggenerally concludes in December, before bowhead whales arrive in January. The snow crab (*Chionoecetes opilio*) fishery is larger (total allowable catch ~ 24.6 million kg in 2010)and extends from the Pribilof Islands to the vicinity of St. Matthew Island, as far as 60° N (~ 40 km south of St. Matthew Island). This fisheryopens on 15 October and closes on 31 May the following year; however, most fishingoccurs between January and April, overlapping with tagged whales near St. Matthew Island. In some years, tanner crabs (*C. bairdi*) are also harvested near the Pribilof Islands, but this fisheryis currently closed (Alaska Department of Fish and Game, unpubl. data). There are also crab fisherieswithin Russian waters (ACIA, 2005); however, we have no information regarding their location or timing.

Although there is potential for bowhead whales to come into contact with active crab gear near St. Matthew Island, our findingssuggest that such contact is unlikely. Bowhead whales are generally found in areas characterized by more than 90% concentration of sea ice, typically far from the southern ice margin, in waters too ice-choked for crab boats to set gear. Therefore, "ghost" gear (i.e., lost fishing gear) is probably a larger source of entanglement. Because the Western Arctic stock of bowheads is increasing (George et al., 2004; Zeh and Punt, 2005) despite an annual subsistence hunt of ~40 animals (Suydam and George, 2004), it seems unlikely that fishery-inducedmortality is limiting the population. However, even a low number of entanglements may become unacceptable if other sources of mortality, such as ship strikes, increase. Measures to reduce losses of gear, especially near St. Matthew Island, would minimize entanglements.

Shipping

Over the last three decades, satellite data indicate decreasing sea ice throughout the Arctic (e.g., ACIA, 2005). Model projections indicate the ice-free season in the Bering Sea will increase by three months from its current average of fiveand a half months (~June to November) to a median of eight and a half months (~May to January) by the end of the century (Douglas, 2010). As a result, there is new interest in Arctic shipping lanes (PAME Working Group, 2009). Both the Northwest Passage, which passes through the Canadian Archipelago and along the northern coast of Alaska, and the Northern Sea Route, which passes along the northern coast of Russia, transit the Bering Strait and the Bering Sea. The Northern Sea Route, which heads towards China, may also transit the Anadyr Strait (Fig. 1). Currently, there are no established shipping lanes or protocols, and communications and vessel trafficservices are also lacking (PAME Working Group, 2009). Both the Bering and Anadyr straits will likely require an established routing system for safe passage of ships; the U.S. Coast Guard recently began to study the Bering Strait region to determine what routing measures are appropriate for human safety (U.S. Federal Register 75, November 8, 2010). Such routing measures could also be planned to minimize impacts on marine mammals.

There are no records of bowhead whales being killed by ship strikes, and George et al. (1994) found non-lethal propeller strikes on less than 1% of whales harvested by subsistence whalers. Currently, however, bowhead whales occupy ice-covered waters where little shipping occurs. If shipping increases with declines in sea ice, bowhead whales are expected to be vulnerable to ship strikes much like North Atlantic right whales (*Eubalaena glacialis*). Bowhead whales are closely related to North Atlantic right whales. Both species prey predominantly on concentrations of zooplankton, and they have similar swim speeds. Swim speeds for feeding North Atlantic right whales range from 0.38 to 1.94 m/s (1.4–7.0 km/hr) (Baumgartner and Mate, 2003: Table 3), and we used 1.94 m/s, which was the fastest observed speed for migrating bowhead whales (Zeh et al., 1993), as a threshold velocity for filtering satellite data (see Methods). A major factor preventing the recovery of North Atlantic right whales is believed to be ship strikes. Of 45 documented North Atlantic right whale fatalities between 1970 and 1999, 36% were due to ship strikes (Knowlton and Kraus, 2001). Laist et al. (2001) speculated that North Atlantic right whales may be more vulnerable to ship strikes than other species because they are less attentive to surrounding activity and noise when feeding, nursing, or mating. While bowhead whales have yet to be exposed to heavy ship traffic, they are known to be more tolerant of industrial activity, such as seismic surveys, while they are feeding (Koski et al., 2009). If bowhead whales, like North Atlantic right whales, are vulnerable to ship strikes, then appropriate planning of shipping lanes may be critical for bowhead whale conservation.

How best to plan shipping routes to minimize potential interactions with bowhead whales will depend upon when shipping traffic occurs. Bowhead whales are currently found within both the Bering and Anadyr straits by the end of November; if the Bering Sea remains ice-free until January, bowhead whales may be exposed to shipping traffic. However, the timing of long-distance shipping may be restricted by sea ice or weather in other seas. For example, the shelf waters in the Chukchi Sea are predicted to be ice-free for only three months, August to October, by mid-century (Douglas, 2010). If long-distance shipping ceases by October, when most of the Western Arctic stock is located in the Chukchi Sea within 80 km of the northern coast of Russia (Quakenbush et al., 2010), then managing shipping lanes may be more important in the Russian Arctic than in the Bering Sea. However, local ship traffic associated with petroleum development and mining is also predicted to increase (ACIA, 2005). Local traffic will not be dependent upon ice conditions farther north and may extend into winter. Model predictions indicate that sea ice will continue to cover the Chukchi and northern Bering seas each winter (Douglas, 2010). The majority of tagged whales migrated out of the Bering Sea and into the Beaufort Sea in relatively heavy ice concentrations, presumably before the future shipping season would begin. Therefore, planning shipping lanes to minimize bowhead-vessel interactions will likely be more important in fall than in spring for the Western Arctic stock.

In the Bering Sea, areas with the highest potential for ship strikes are the confined regions of the Bering and Anadyr straits. During the southern migration, virtually all tagged whales migrated on the western side of the Bering Strait, between Big Diomede and Cape Pe'ek (Fig. 3). Routing ship traffic to the eastern side of the Bering Strait, between Little Diomede and Wales, in fall and implementing speed restrictions would minimize the probability of ship strikes. To date, most tagged bowhead whales (20 of 21) have migrated through the Anadyr Strait, on the western side of St. Lawrence Island (Fig. 4). Therefore, routing ship traffic east of St. Lawrence Island in fall would likely be better for bowhead whales than allowing traffic to pass through the Anadyr Strait.

In summary, we have described and contrasted the winter distribution of bowhead whales during two winters, 2008–09 and 2009–10. Although a larger and perhaps more representative sample of whale movements may lead to modification of our description of bowhead distribution within the Bering Sea, the areas where human-whale conflict will likely occur are clear. Interactions with commercial fishing or crabbing may occur at the marginal ice edge, but there is no evidence that the level of interactions is currently a conservation concern for the increasing Western Arctic stock. However, this situation may change if fisheries shift north with retreating sea ice and the number of entanglements increases, or if other sources of mortality, such as ship strikes, increase and the cumulative impacts reach a level of concern. The two areas that should now receive management attention within the Bering Sea are the Bering and Anadyr straits. Shipping lanes are currently being planned for these relatively narrow straits through which large numbers of whales migrate each spring and fall, and information on bowhead whale movements should prove invaluable in developing mitigation measures.

ACKNOWLEDGEMENTS

This cooperative project involved contributions and hard work from many organizations, agencies, and individuals including the following: the Alaska Eskimo Whaling Commission, the North Slope Borough (Robert Suydam, Ambrose Leavitt, and Taqulik Hepa), the Barrow and Kaktovik Whaling Captain's Associations (Eugene Brower, Fenton Rexford, Joe Kaleak, George Tagarook, and Eddie Arey), the Barrow Arctic Science Consortium, the Aklavik and Tuktoyaktuk Hunters and Trappers Committees (Dennis Arey, Larry Arey, Pat Kasook, Buddy Gruben, Douglas Panaktalok, Mikkel Panaktalok, Max Kotokak, Sr., Charles Pokiak, and James Pokiak), the Department of Fisheries and Oceans Canada (DFO) (Lois Harwood, Kevin Bill, Tim Leblanc, Patrick Ryan, Terry Stein, and Angus Alunik), Dr. Stephen Raverty of the Animal Health Centre (Government of British Columbia), the Greenland Institute of Natural Resources, and Mikkel and Anders Villum Jensen. Funding for this research was provided by the United States Minerals Management Service (now Bureau of Ocean Energy Management) with superior support and assistance from Charles Monnett. Much of the tagging operation in Canada was funded by the Fisheries Joint Management Committee, the Ecosystem Research Initiative (DFO), and the Panel for Energy Research and Development, with extensive support and coordination from Lois Harwood. Bowhead whale research has been conducted in the U.S. under a Marine Mammal Protection Act permit issued to National Marine Fisheries Service (No. 782-1719) and under two Alaska Department of Fish and Game's Animal Care and Use permits (Nos. 06-16 and 09-21). In Canada, research was conducted under the Department of Fisheries and Oceans Scientific License Nos. S-07/08-4007-IN, S-08/09-4000-IN, S-09/10-4005-IN-A1 and Animal Care Protocols FWI-ACC-2007-2008-013, FWI-ACC-2008-031, and FWI-ACC-2009-019.

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